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**Journal of Applied Ecology**

*DOI:*
10.1111/1365-2664.12811

Published: 01/06/2017

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*
Pardal-Souza, A., Dias, G., Jenkins, S., Ciotti, A., & Christofoletti, R. (2017). Shading impacts by coastal infrastructure on biological communities from subtropical rocky shores'. *Journal of Applied Ecology*, *54*(3), 826-835. https://doi.org/10.1111/1365-2664.12811

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05. May. 2023

# Shading impacts by coastal infrastructure on biological communities from subtropical rocky shores

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**Running title:** Effect of shading on biological communities

## Summary

**1.** Artificial shading has been highlighted as an important human disturbance, affecting both productivity and community organisation. However, studies of shading have been poorly explored from an environmental impact perspective.

**2.** We compared community structure on subtropical rocky shores in areas shaded by human constructions with those in unshaded areas. We then implemented a manipulative field experiment to determine the effects of shading on the macrobenthic community, biofilm biomass and larval recruitment.

**3.** Shading consistently affected the biological community of rocky shores. The biomass and cover of macroalgae and the size of most sedentary grazers were smaller in shaded habitat. In the infralittoral fringe, we recorded a shift in dominance from macroalgae in unshaded habitats to invertebrate filter-feeders in shaded ones. In a similar way, the community from the mesolittoral was also affected by shading but not at all locations.

**4.** Experimental manipulation of shading led to a total loss of macroalgae from the infralittoral fringe and no community replacement over a period of 220 days. In the mesolittoral, oysters became more abundant in shaded conditions, while barnacles decreased in abundance. Larval recruitment was also affected, with oysters and barnacles recruiting more in shaded habitats.

**5.** *Synthesis and applications*. We demonstrate a clear impact of shading by artificial man-made structures on patterns and processes regulating biodiversity on rocky shores and thus consequences for coastal ecosystem functioning. We argue that shading by artificial coastal structures, such as those proposed in the port expansion in our study site in south-eastern Brazil, are potentially under-

estimated. Our work emphasises the importance of careful evaluations of artificial structures in order to promote sustainable coastal development. As a result, we do not recommend the proposed expansion by suspended structures of the port of São Sebastião, as the consequent shading will negatively affect the biodiversity and ecosystem functioning of the Araçá Bay and surrounding areas.

**Key-words:** Araçá Bay, biofilm, filter-feeder invertebrates, grazers, human disturbances, intertidal, larval recruitment, luminosity, macroalgae, port expansion.

## Introduction

Sunlight shading affects the structure and functioning of biological communities in natural ecosystems, through a reduction in the incidence of solar radiation, thus disturbing the growth and biomass production by autotrophs in both terrestrial (Williams, Messier & Kneeshaw 1999; Pagès *et al*. 2003) and aquatic environments (Fitzprack & Kirkman 1995; Quinn *et al.* 1997; Ruiz & Romero 2001). Sunlight limitation can influence animal communities by affecting physical conditions (e.g., reducing heat stress) (Williams 1994; Kon, Kurokura & Tongnunui 2010), decreasing energetic resources of herbivores (Hill, Ryon & Schilling 1995; Harley 2002) and influencing larval recruitment of marine organisms (Thorson 1964; Saunders & Connell 2001; Blockley & Chapman 2006).

In both freshwater and marine environments, sunlight shading occurs naturally due to riparian vegetation (Beschta 1997) or macroalgae coverage (Clark, Edwards & Foster 2004). However, sunlight can also be blocked by man-made structures, such as bridges, piers, wharfs, docks and ports. Although the influence of the additional substrate provided by such structures on aquatic biodiversity has been addressed (Bulleri & Chapman 2010), their role in artificial shading has been overlooked. Results derived from salt marshes (Sanger, Holland & Gainey 2004; Struck *et al.* 2004), seagrass beds (Burdick & Short 1999; Shafer 1999), estuaries (Able, Manderson & Studholme 1998) and hard substrates (Glasby 1999; Blockley 2007) consistently show negative effects of shading by artificial structures on autotrophs and alterations in the structure of biological communities. Specifically on hard substrates, artificial shading has been associated with shifts in the structure and the diversity of the community, by reducing macroalgae cover (Glasby 1999; Blockley & Chapman 2006; Blockley 2007; Miller & Etter 2008) and also by increasing the overall abundances of some filter-feeding invertebrates and mobile consumers (Williams 1994; Glasby 1999; Takada 1999; Blockley 2007; Miller & Etter 2008).

The accelerating urbanisation of coastal areas worldwide is well recognised (Small & Nicholls 2003; NOAA 2004; EEA 2006). Intensification of international commercial trade has increased the demand for construction or expansion of ports and associated infrastructure (Van Gils & Klijn 2007; Hricko 2012). Such projects are usually of great magnitude and cause substantial disturbance to the natural environment where they are installed and in nearby locations. Loss of habitat and biodiversity, contamination by toxic substances, introduction of exotic species and deterioration of air and water quality (Darbra

& Casal 2004; Gupta, Gupta & Patil 2005; Grech *et al.* 2013) are some examples of potential impacts of ports. Quantifying the potential effects of such urban structures on the organisation and functioning of biological communities of natural ecosystems, has gained importance over the past decade, not only from an academic viewpoint, but as tools for coastal management (Bulleri & Airoldi 2005; Perkol-Finkel *et al.* 2012; Ferrario *et al.* 2016). However, in considering the impacts of coastal development the effects of enhanced shading, although recognised, are potentially under-estimated and have received far less attention than other sources of disturbance.

On the north coast of São Paulo State, Brazil, the expansion of the port of São Sebastião has been discussed for many decades (see Appendix S1 in supplementary information for details). The initial proposal was to increase port facilities through infilling of an adjacent area, Araçá Bay (Fig. S1). However, this small bay is a hot spot for benthic biodiversity in the Southwest Atlantic (Amaral *et al.* 2010, 2015), and after some debate, it was proposed to avoid infilling of the bay by construction of a structure suspended by pillars, covering 75% of Araçá Bay. Among other disturbances, such plans would substantially restrict sunlight to natural habitats. As a consequence we aimed to assess the effects of shading on the rocky intertidal benthic community. Through a descriptive and manipulative approach, we tested the hypotheses that shading (i) decreases abundance or biomass of primary producers; (ii) reduces body size of sedentary grazers, owing to bottom-up control from a reduced biofilm; and (iii) modifies the organisation of sessile macrobenthic communities through effects on autotrophs and on larval recruitment. We show consistent impacts, based on observational surveys and experimental manipulation, of sunlight shading on patterns and

processes driving structure and functioning of biological communities of the rocky intertidal, supporting the importance of the careful considerations of shading disturbance in discussions regarding sustainable development and policies for expansion of ports and man-made structures worldwide.

## Material and methods

### DESCRIPTIVE APPROACH

In September 2014, a survey was conducted in three subtropical sheltered rocky shores in the Southwest Atlantic that are partially shaded by man-made constructions, built at least five years before the study. Tidal range for the sites is about 1.4 m (Fig. S1; Table S1). All shores are dominated by filter-feeding invertebrates (e.g., barnacles, oysters and mussels) in the mesolittoral, while macroalgae (e.g., corticoid and turf forming algae) dominate the infralittoral fringe. Biological data were compared between two different habitats within each of the three shores: (i) unshaded, naturally sunny areas; and (ii) shaded, sunlight-restricted areas due to human-made structures. In the shaded habitat, we sampled the area under the structure where no direct sunlight reached the substrate. An area of approximately 50 m horizontal distance was sampled in each habitat; these areas of shore were immediately adjacent to each other (separated by 20 m) to avoid any differences in physical environment such as degree of wave exposure. Response variables measured included the biomass of primary producers, population structure of sedentary grazers and sessile community organization.

143 **Primary producers.** Biofilm biomass was estimated by a field-based remote
144 sensing method using digital photographs (adapted from Murphy *et al.* 2005;
145 Murphy & Underwood 2006; Murphy, Underwood & Jackson 2009; see
146 Appendix S2 in supplementary materials for details). Ten images, each of 100
147 $cm^2$, were haphazardly taken in the upper mesolittoral of each location in
148 unshaded and shaded habitats. Macroalgal biomass was estimated by
149 destructive sampling. Five areas of 100 $cm^2$ in the infralittoral fringe in both
150 habitats on the three shores were scraped clear and the macroalgae collected
151 were dried at 60$^o$ C for 24h and weighed. The dry material was then burned at
152 500$^o$ C for 4h and we calculated the ash free dry weight.

153

154 **Sedentary grazers.** Population structure of three benthic grazers - the limpet
155 *Lottia subrugosa* (d'Orbigny 1846) in the lower mesolittoral and the littorinid
156 gastropods *Echinolittorina lineolata* (d'Orbigny 1840) and *Littoraria flava* (King
157 1832) in the upper mesolittoral was assessed through photography using
158 quadrats of 100 $cm^2$ (n = 20 per habitat) for *L. subrugosa* and 25 $cm^2$ (n = 10
159 per habitat) for littorinids. Due to the small body size, the littorinids were
160 collected and, photographed in the field on a white background to facilitate
161 counting and measurement. Size was defined as the longest length of the shell.
162 Comparisons of body size of consumers between unshaded and shaded areas
163 were performed only when we obtained at least 50 specimens in each habitat
164 on each shore.

165

166 **Community organization.** Sessile macrobenthic communities were compared
167 between unshaded and shaded habitats in three tidal zones: infralittoral fringe,

lower mesolittoral and upper mesolittoral, delimited according to Christofoletti *et al.* (2011). Samples were taken haphazardly through photography (100 cm², n = 10 or 20 per habitat) and taxa abundance estimated as percentage cover using 100 regular intersection grids. Macroalgae were classified into functional groups, according to Littler & Arnold (1982) and Littler, Litter & Taylor (1983). Other taxa were identified to the lowest possible taxonomic group. We also compared the abundance of the functional groups 'macroalgae' and 'filter-feeding invertebrates' between different habitats to test the hypothesis of a dominance shift in the infralittoral fringe due to shading.

MANIPULATIVE APPROACH

Experimental manipulations to test the effect of shading on biofilm biomass and community organization were conducted on the shore of Pernambuco island, within Araçá Bay (São Sebastião, São Paulo State, Brazil; Fig. S1). The experiment lasted 221 days in two intertidal zones (infralittoral fringe and upper mesolittoral) and was performed with three treatments: (i) shaded, constructed with marine plywood sheets (40 x 40 cm) suspended 10 cm above the substrate by stainless steel bars in each corner; (ii) procedural control, provided by transparent acrylic sheets, mimicking the physical structure of the shaded treatment but allowing sunlight penetration to the substratum (≈ 90%); and (iii) control, unmanipulated areas. While all the 40 x 40 cm area is under the influence of the treatment we only used the central 100 cm² for analyses, to avoid artefacts caused by diffuse light at the perimeter. Although partial shading (diffuse light) is a natural consequence of many artificial structures our manipulative approach intended to simulate the effect of full

193 shade expected following potential port expansion We deployed 5 replicates of
194 each treatment in each intertidal zone. Replicates were separated by at least 2
195 m and the treatments were randomly allocated within each tidal zone. Acrylic
196 plates were regularly cleaned and damaged structures were replaced as soon
197 as possible. To test the efficacy of manipulations, luminosity and temperature
198 sensors were deployed on treatments at both tide heights. Both luminosity and
199 temperature were reduced by shading, but did not differ between control
200 treatments (more details in Appendix S3).

201 Biofilm biomass was evaluated in the upper mesolittoral using the same
202 remote sensing technique and protocols (Appendix S2). Samples were
203 undertaken 0, 15, 29, 44, 73, 149, 191 and 220 days after the start of the
204 experiment. Benthic community composition was sampled on the same dates in
205 the upper mesolittoral and, after 0, 15, 29, 75, 191 and 221 days in the
206 infralittoral fringe, as allowed by tidal conditions. Because communities were
207 dominated by a few species during the whole experiment, we tested how the
208 treatments affected the areas covered by macroalgae, oysters, the barnacle
209 *Chthamalus bisinuatus* (Pilsbry 1916) and open space.

210

211 **Larval recruitment.** To test whether alterations in adult populations were linked
212 to effects of shading on larval recruitment, we utilized acrylic plates (8 x 8 cm)
213 covered with gray slip-resistant tape (3M$^{TM}$ Safety-Walk, Minnesota, EUA).
214 Plates were screwed in the upper mesolittoral, under the procedural control and
215 shaded treatments, avoiding central sampling area, and close to replicates in
216 control. Plates were replaced approximately every 30 days. In the laboratory,
217 we identified and quantified recruits under a stereomicroscope. We tested the

effects of time and treatment on the recruitment rate (number of recruits per days in the field) of barnacles and oysters, the two most abundant taxa in the upper mesolittoral.

## DATA ANALYSIS

In the descriptive approach, ecological parameters from primary producers, sedentary grazers and univariate data from benthic community (combined macroalgae and filter-feeding invertebrates) were analyzed using factorial ANOVA, considering the factors ‘habitat’ (fixed, 2 levels: unshaded and shaded) and ‘location’ (random, 3 levels). Specifically for the analysis of body size of *Lottia subrugosa* and *Echinolittorina lineolata*, location had 2 levels as we did not sample enough specimens at one of the shores. Variance homogeneity was tested by Cochran’s procedure and transformations were applied when needed. Where heterogeneous variances persisted, the same procedure was still performed using raw data, and attention is drawn to the potential for increased probability of type I errors in these cases. Body size of *Littoraria flava* was compared through a t-test after confirming homoscedasticity (Levene’s test), since we sampled this species in enough number only in one shore.

Data from the sessile macrobenthic communities were converted to a similarity matrix based on Bray-Curtis distance and compared between ‘habitat’ (fixed, 2 levels: unshaded and shaded) and ‘location’ (random, 3 levels) using PERMANOVA test (999 permutations) (Anderson 2001). Comparisons of communities from different habitats within locations were performed by post-hoc pair-wise tests. Non-metric multidimensional scaling (nMDS) was used for

visualization of data. SIMPER analysis was applied to identity the taxa which contributed most to dissimilarity between habitats.

In the experimental approach, repeated measures ANOVA was used to assess the differences between treatments through time on biofilm biomass, area covered by macroalgae, oysters, barnacle *Chthamalus bisinuatus* and open space. Mauchly's sphericity test was applied to verify time autocorrelation. When this assumption was violated, we corrected statistical significances with Greenhouse-Geisser adjustment. Post-hoc Student-Newman-Keuls (SNK) test was used for multiple comparisons of means for both statistical techniques. The effects of 'treatment' and 'time' (random factor) on recruitment rate during the manipulative approach were evaluated using a factorial ANOVA.

## Results

### DESCRIPTIVE APPROACH

#### Primary producers

There was no influence of shading on biofilm biomass on shores under the influence of man-made constructions (Table 1). On the other hand, shading decreased the macroalgal biomass, which was about eight times lower in the shaded (mean ± SE: 1.01 ± 0.43 g) than in the unshaded habitat (8.33 ± 1.28 g) (Table 1).

#### Sedentary grazers

Shading affected body size of the limpet *Lottia subrugosa* and the littorinids *Echinolittorina lineolata* (Table 1) and *Littoraria flava* (t-test, df = 121, t = 5.36, $P < 0.001$) (Fig. 1). Grazers from four of the five sampled populations were smaller in the shaded habitat, although, *L. subrugosa* in one of the localities was bigger in shaded habitat (SNK 'Habitat x Location' interaction: Table 1).

There was a general trend across all three species at all shores for greater abundance in unshaded areas (Fig 1). However only for *Echinolittorina lineolata*, on one rocky shore, was this effect of shade significant (SNK 'Habitat x Location' interaction: Table 1; Fig. 1).

Community organization

There was a significant, although spatially variable, effect of shading on community organization. In the infralittoral fringe, there was a significant effect of shading at all three shores, while the effect was significant on two shores in the lower mesolittoral and one shore in the upper mesolittoral (Post-hoc pair-wise test 'Habitat x Location' interaction: Table 2; Fig. 2).

In the infralittoral fringe, cover of combined macroalgae decreased from about 70% in unshaded habitat to 17% in shaded habitat. On the other hand, combined invertebrate filter-feeders increased from 5% in unshaded to 65% in shaded habitats (ANOVA, effect of 'Habitat', macroalgae: $F_{1,54} = 23{,}470.89$; filter-feeding invertebrates: $F_{1,54} = 491.84$; $P < 0.01$). Macroalgae morphofunctional groups combined were responsible for more than 45% of dissimilarity between habitats (SIMPER: Table S2). For both other zones, while

289 the same species occurred in shaded and unshaded habitats, the relative
290 abundance of organisms was affected by shading (SIMPER: Table S2). In the
291 lower mesolittoral, oysters were more abundant in shaded than in unshaded
292 areas, while *Brachidontes* sp. showed an opposite pattern. These two species
293 contributed 55% of the dissimilarity between the sessile communities from
294 shaded and unshaded habitats at this shore height. In the upper mesolittoral,
295 the barnacle *Microeuraphia rizophorae* (De Oliveira 1940) was more abundant
296 in shaded than in unshaded habitats, while *Chthamalus bisinuatus* showed an
297 opposite pattern. These two species contributed 91% of the dissimilarity
298 between the sessile communities from shaded and unshaded habitats in the
299 upper mesolittoral.

300

301 MANIPULATIVE APPROACH

302 Biofilm biomass

303 Biofilm biomass showed a high degree of variation among replicates and
304 over time (Fig. 3). Although there was a significant effect of treatment (Table 3),
305 this was a consequence of the control being placed in plots of higher NDVI at
306 the start of the experiment (Fig. 3). There was no significant interaction between
307 treatment and time which might indicate divergence of the treatments over time
308 (Table 3).

309

310 Community organization

311 In the infralittoral fringe, macroalgae covered almost 100% at the
312 beginning of the experiment and quickly decreased in the shading treatment

during the first 2 months, completely disappearing at day 221 (SNK 'Treatment x Time' interaction: Table 3, Fig. 4). Shading also affected the structure of the macrobenthic community in the upper mesolittoral. In the shaded treatment, oysters increased in abundance from 1.2% at the beginning of the experiment to 37.8% after 220 days, while there was no change in other treatments. Conversely, the barnacle *Chthamalus bisinuatus* decreased in abundance due to shading, reaching a cover of about 10% by the end of the experiment (SNK 'Treatment x Time' interaction: Table 3; Fig. 4).

Larval recruitment

Larval recruitment rate was affected by shade. Oyster larvae recruited more in the shaded treatment than in the control treatments (SNK 'Treatment': Table 4; Fig. 5). For the barnacle *Chthamalus bisinuatus*, larval recruitment was smaller in the control than in shaded and procedural control (SNK 'Treatment': Table 4; Fig. 5). Also, there was variation among sampling dates, with larger numbers of *C. bisinuatus* larvae recruiting in April/2015 than in all 5 months before, which did not differ from one another (SNK 'Time': Table 4).

## Discussion

Many studies have shown how artificial structures can influence local ecosystems by the addition of substrate (see Bulleri & Chapman 2010 for review). We showed important ecological changes on natural rocky substrates associated with such structures and demonstrated through experiments that the changes were a consequence of shading. Under shading disturbance, biomass

of primary producers, body size of primary consumers, community structure and larval recruitment changed, and the results were consistent for both descriptive and manipulative approaches. The changes in communities are likely explained by physical factors and biological processes such as competition, recruitment rates and physiological status of the organisms, as discussed below. Our observational and experimental results contribute quantitatively to the extensive debate on coastal management under pressure from urbanization (Bulleri & Chapman 2010; Dugan *et al.* 2011).

The results highlighted more pronounced changes in the intertidal communities found at the lower levels in the shore, suggesting that this zone is more vulnerable to shading. There was a strong negative influence of shading on macroalgae, expected since light restriction limits photosynthesis and prevents autotrophs survival, as observed for other ecosystems (e.g., Glasby 1999; Shafer 1999; Struck *et al*. 2004; Blockley 2007; Miller & Etter 2008). Surveys showed that in areas shaded by human-made structures, macroalgae coverage and biomass were low, while experimental manipulation of shade caused progressive loss of existing macroalgae, with total loss in about 6 months. Differences in abundance of macroalgae between unshaded and shaded habitats can also be linked to recruitment, as macroalgae tend to recruit less in light-limited areas (Clark, Edwards & Foster 2004; Blockey & Chapman 2006) due to high post-settlement mortality of spores and low growth (Goldberg & Foster 2002).

With the reduction in macroalgae in the infralittoral zone affected by man-made structures, dominance shifted toward filter-feeding invertebrates. This shift to invertebrates was not observed following shade manipulation, possibly

as a consequence of limited recruitment over the 220 day experimental period, but also potentially owing to high mortality of early settlers caused by sedimentation observed in experimental plots (Airoldi 2003). It was not clear the extent to which such sedimentation was an artefact of the shade structures, since sedimentation on rock throughout Araçá Bay is common depending on prevailing weather and sea conditions. Whether shading leads to dominance by filter feeding invertebrates, or to open bare space, there was a clear reduction in local biodiversity, considering the loss of macroalgae species and their associated fauna (Christie, Norderhaug & Fredriksen 2009). An additional consequence of loss of turf macroalgae cover is the opening up of bare space and an enhanced probability of invasive species establishment (Arenas *et al.* 2006). This shading may be an additional mechanism by which urban infrastructure in port facilities can facilitate the introduction and spread of exotic species (Bulleri & Airoldi 2005; Vaselli, Bulleri & Benedetti-Cecchi 2008; Dafforn, Johnston & Glasby 2009).

We predicted, based on previous observations (Hill, Ryon & Schilling 1995; Harley 2002), that shading would have a negative effect on the intertidal epilithic biofilm, but we found no support for this hypothesis. The intertidal biofilm is a complex system and the influence of light on its dynamics is still controversial. Biofilm biomass can increase due to shading or reduced sunlight regimes (Jenkins *et al.* 2001; Thompson, Norton & Hawkins 2004) or show restricted growth when exposed to excess sunlight, due to photoinhibition or thermal stress (Serôdio, Vieira & Cruz 2008; Coelho, Vieira & Serôdio 2009). Also, it is important to note that our manipulation did not exclude biofilm grazers. Previous work in the study region has shown that fast-moving grazers

mask the effect of sedentary grazers on biofilm, while grazing pressures of both together mask environmental influences (Christofoletti, Almeida & Ciotti 2011). Although the influence of shading on biofilm was not seen, our prediction of negative shade effects on grazers was confirmed at most locations. Another, non-exclusive hypothesis to explain bigger animals in sunny habitats is that grazer size is related to increased heat stress in sunny habitats, which would select specimens with larger shells due to optimized water storage (Vermeij 1973; Tanaka, Duque-Estrada & Magalhães 2002) and also increasing growth rate due a higher metabolism (Chelazzi, Williams & Gray 1999).

Shading can also promote differences between communities by changing the recruitment regime (Chapman & Blockley 2006). Many late-stage larvae show active choice at settlement (Keough & Downes 1982); available light is an important cue with many larvae of marine organisms exhibiting negative phototactic behaviour, thus settling in light-limited habitats (Thorson 1964; Young & Chia 1984; Saunders & Connell 2001). Blockley & Chapman (2006) showed that shading increased recruitment of some filter-feeding invertebrates but reduced macroalgae recruitment on seawalls. Such results are consistent with the abundance of these taxa in established shaded communities in the present study, supporting the conclusion that changes in community organisation in the infralittoral fringe and mesolittoral following shading may be linked to larval recruitment. Oysters became more abundant in the upper mesolittoral in the shaded treatment and barnacle recruitment increased in shaded habitats. However, interestingly, the abundance of adult barnacles reduced under shading. Such patterns, both in the natural environment and experiments indicate the need to differentiate between effects of shade on

412 settlement/ early post settlement mortality and the development of adult
413 populations.

414 Our study shows the consequences of shading from artificial structures
415 on the biota of intertidal rocky shores. Coastlines worldwide are being
416 increasingly modified through constructions ranging from artificial sea defences
417 to port facilities (Bulleri & Chapman 2010; Dugan *et al.* 2011). Such urban
418 infrastructures alter landscape via loss, addition or fragmentation of habitat
419 (Chapman 2006; Goodsell, Chapman & Underwood 2007), and modify
420 biodiversity, since artificial and natural habitats do not support the same
421 communities (Bulleri & Chapman 2004). Our study was prompted by the
422 proposal for expansion of the port of São Sebastião which would result in a
423 shaded area of approximately 1 $km^2$ of the Araçá Bay, impacting rocky shores,
424 soft sediment habitats and mangroves. Results indicate such a development
425 would cause substantial decreases in macroalgae cover on hard substrate
426 leading to a reduction in primary production, carbon exchange and habitat for
427 associated fauna. Shading is also predicted to increase filter-feeding
428 invertebrate cover strongly influencing the dynamics of the pelagic environment.
429 The Araçá Bay, like many other coastal sites threatened by development is a
430 hot spot in marine biodiversity (Amaral *et al.* 2010, 2015) supporting a wide
431 range of ecosystem services. Understanding the impact of shading contributes
432 to a wider view of the consequences of such development and hence informs
433 discussions regarding sustainable development, in this and other regions
434 around the world. Specifically regarding the expansion plans of the port of São
435 Sebastião, our results suggest that covering the bay with a suspended structure
436 will have major negative effects on biodiversity and ecosystem functioning. As a

result, we recommend that stakeholders carefully evaluate the expansion plan, and, based on the likely shade effects (as well as many other potential impacts) across much of the bay, we do not recommend it.

## Acknowledgments

This work was supported by research funds granted by São Paulo Research Foundation (FAPESP) to A.L.P.S (#2013/19122-0), to A.M.C (#2013/50199-8), to R.A.C. (#2013/11594-9) and to Biota Araçá Project (#2011/50317-5). We thank Deborah, Jaqueline, Gabriella, Neemias, Ivan, Elso and Joseilto for support with field work. Finally, we are grateful to Isabella and A.C.Z Amaral for help with some figures, and to M.O. Tanaka, G.H. Pereira-Filho and the anonymous referees for their valuable comments on the manuscript.

## Data accessibility

- Study sites locations: uploaded as online supporting information (Table S1).

- Data archived in Figshare https://dx.doi.org/10.6084/m9.figshare.3205285.v1 (Pardal-Souza *et al.* 2016).

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## Supporting Information

TABLES

**Table 1.** Effect of habitats (unshaded and shaded) (2-way ANOVA) on primary producers and sedentary grazers on subtropical rocky shores. ***P* < 0.01; ****P* < 0.001; ns = not significant. §Data transformed to ln (x +1)

| Effect | df | MS | F | *P* | df | MS | F | *P* |
|---|---|---|---|---|---|---|---|---|
| | | | Primary producers | | | | | |
| | | Biofilm biomass | | | Macroalgae biomass | | | |
| Habitat = H | 1 | 0.004 | 0.16 | 0.72 | 1 | 4.02 | 137.25 | ** |
| Location = L | 2 | 0.094 | 3.84 | 0.20 | 2 | 0.49 | 16.92 | 0.05 |
| H*L | 2 | 0.024 | 2.92 | 0.06 | 2 | 0.03 | 0.25 | 0.78 |
| Error | 54 | 0.008 | | | 24 | 0.11 | | |
| Cochran's test | | C = 0.47 (***) | | | | C = 0.45 (ns) | | |
| | | | Grazers body size | | | | | |
| | | *L. subrugosa* | | | *E. lineolata* | | | |
| Habitat = H | 1 | 0.52 | 0.001 | 0.97 | 1 | 34.66 | 3.28 | 0.32 |
| Location = L | 1 | 11.52 | 0.027 | 0.89 | 1 | 38.18 | 3.61 | 0.30 |
| H*L | 1 | 416.12 | 42.56 | *** | 1 | 10.55 | 11.95 | *** |
| Error | 1066 | 9.77 | | | 606 | 0.88 | | |
| Cochran's test | | C = 0.51 (***) | | | | C = 0.39 (***) | | |
| | | | Grazers abundance | | | | | |
| | | *L. subrugosa* | | | *E. lineolata*§ | | | |
| Habitat = H | 1 | 2,226.05 | 5.26 | 0.26 | 1 | 1.97 | 2.17 | 0.28 |
| Location = L | 1 | 61.25 | 0.14 | 0.76 | 2 | 2.99 | 3.30 | 0.23 |
| H*L | 1 | 423.20 | 3.37 | 0.07 | 2 | 0.90 | 9.79 | *** |
| Error | 76 | 125.46 | | | 54 | 0.09 | | |
| Cochran's test | | C = 0.47 (***) | | | | C = 0.28 (ns) | | |

**Table 2.** Effects of habitats (unshaded and shaded) (PERMANOVA) on sessile macrobenthic communities on different zonation ranges in subtropical rocky shores. All data was transformed to arcsine ($\sqrt{x}$) + 1. ***$P$ < 0.001

| Effect | df | MS | Pseudo-F | $P$ | df | MS | Pseudo-F | $P$ | df | MS | Pseudo-F | $P$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | (a) Infralittoral fringe | | | | (b) Lower mesolittoral | | | | (c) Upper mesolittoral | | |
| Habitat = H | 1 | 315.96 | 1.77 | 0.24 | 1 | 138.69 | 0.55 | 0.60 | 1 | 150.98 | 0.63 | 0.57 |
| Location = L | 2 | 156.02 | 7.36 | *** | 2 | 1,521.10 | 147.30 | *** | 2 | 376.64 | 21.03 | *** |
| H*L | 2 | 177.87 | 8.40 | *** | 2 | 252.02 | 26.06 | *** | 2 | 240.12 | 13.41 | *** |
| Error | 54 | 21.17 | | | 114 | 1,102.40 | | | 54 | 17.91 | | |
| | | Pair-wise tests ‘unshaded’ *vs.* ‘shaded’ inside Location | | | | | | | | | | |
| | | (a) Infralittoral fringe | | | | (b) Lower mesolittoral | | | | (c) Upper mesolittoral | | |
| | | t | $P$ | | | t | $P$ | | | t | $P$ | |
| | RS1 | 3.06 | *** | | | 1.02 | 0.36 | | | 1.44 | 0.16 | |
| | RS2 | 3.43 | *** | | | 4.84 | *** | | | 5.31 | *** | |
| | RS3 | 3.30 | *** | | | 4.69 | *** | | | 0.40 | 0.80 | |

**Table 3.** Effects of treatments (repeated measures ANOVA) on abundance of primary producers, sessile invertebrates and open space on shading manipulation in the upper mesolittoral and infralittoral fringe. *$P$ < 0.05; **$P$ < 0.01; ***$P$ < 0.001; *§ P*-values corrected by Greenhouse-Geisser adjustment. All response variables except biofilm were transformed to arcsine ($\sqrt{x}$)

| Effect | df | MS | F | *P* | MS | F | *P* | MS | F | *P* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Upper mesolittoral | | | | | | | |
| | | Biofilm | | | Oysters§ | | | *C. bisinuatus*§ | | |
| Treatment = Tr | 2 | 0.0240 | 8.87 | ** | 0.60 | 12.31 | *** | 0.62 | 4.13 | * |
| Error | 12 | 0.0028 | | | 0.05 | | | 0.15 | | |
| Time = Ti | 7 | 0.0058 | 3.79 | ** | 0.02 | 1.48 | 0.25 | 0.70 | 50.40 | *** |
| Tr*Ti | 14 | 0.0021 | 1.36 | 0.19 | 0.10 | 6.45 | ** | 0.05 | 4.10 | ** |
| Error | 84 | 0.0015 | | | 0.01 | | | 0.01 | | |
| | | | Infralittoral fringe | | | | | | | |
| | | Macroalgae | | | | Open space | | | | |
| Treatment = Tr | 2 | 5.75 | 64.22 | *** | 5.16 | 61.05 | *** | | | |
| Error | 12 | 0.09 | | | 0.08 | | | | | |
| Time = Ti | 5 | 0.98 | 30.87 | *** | 0.94 | 29.09 | *** | | | |
| Tr*Ti | 10 | 0.34 | 10.64 | *** | 0.32 | 10.03 | *** | | | |
| Error | 60 | 0.03 | | | 0.03 | | | | | |

**Table 4.** Effects of treatments (2-way ANOVA) on recruitment rate of oysters and the barnacle *Chthamalus bisinuatus* on shading manipulation in the upper mesolittoral. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

| Effect | df | MS | F | *P* | MS | F | *P* |
|---|---|---|---|---|---|---|---|
| | *Chthamalus bisinuatus* | | | | Oysters | | |
| Treatment = Tr | 2 | 0.98 | 10.97 | ** | 0.48 | 5.32 | * |
| Time = Ti | 5 | 1.34 | 15.01 | *** | 0.10 | 1.07 | 0.42 |
| Tr*Ti | 10 | 0.09 | 0.84 | 0.58 | 0.09 | 1.79 | 0.07 |
| Error | 72 | 0.10 | | | 0.05 | | |
| Cochran's test | C = 0.25 (***) | | | | C = 0.83 (***) | | |

FIGURE CAPTIONS

**Fig. 1.** Body size and abundance (mean + standard error) of sedentary grazers (a) *Lottia subrugosa*, (b) *Echinolittorina lineolata* and (c) *Littoraria flava* in unshaded and shaded habitats in subtropical rocky shores (RS). *$P < 0.01$; ***$P < 0.001$; ns = not significant; according to SNK test (items *a* and *b*) or t-test (*c*).

**Fig. 2.** nMDS diagrams of macrobenthic communities of different zonation ranges in unshaded and shaded habitats in subtropical rocky shores (RS).

**Fig. 3.** Biofilm biomass (NDVI) (mean ± standard error) in treatments of shading manipulation in the upper mesolittoral.

**Fig. 4.** Cover percentage (mean ± standard error) of macroalgae, open space, oysters and the barnacle *Chthamalus bisinuatus* in treatments of shading manipulation. Post-hoc comparisons of treatments shown only for beginning and end of experiment. SNK test: ns = not significant; ***control = procedural control ≠ shaded.

**Fig. 5.** Cumulative recruitment (mean number of accumulated recruits in each time) of oysters and the barnacle *Chthamalus bisinuatus* in treatments of shading manipulation.

**FIGURES**

Figure 1

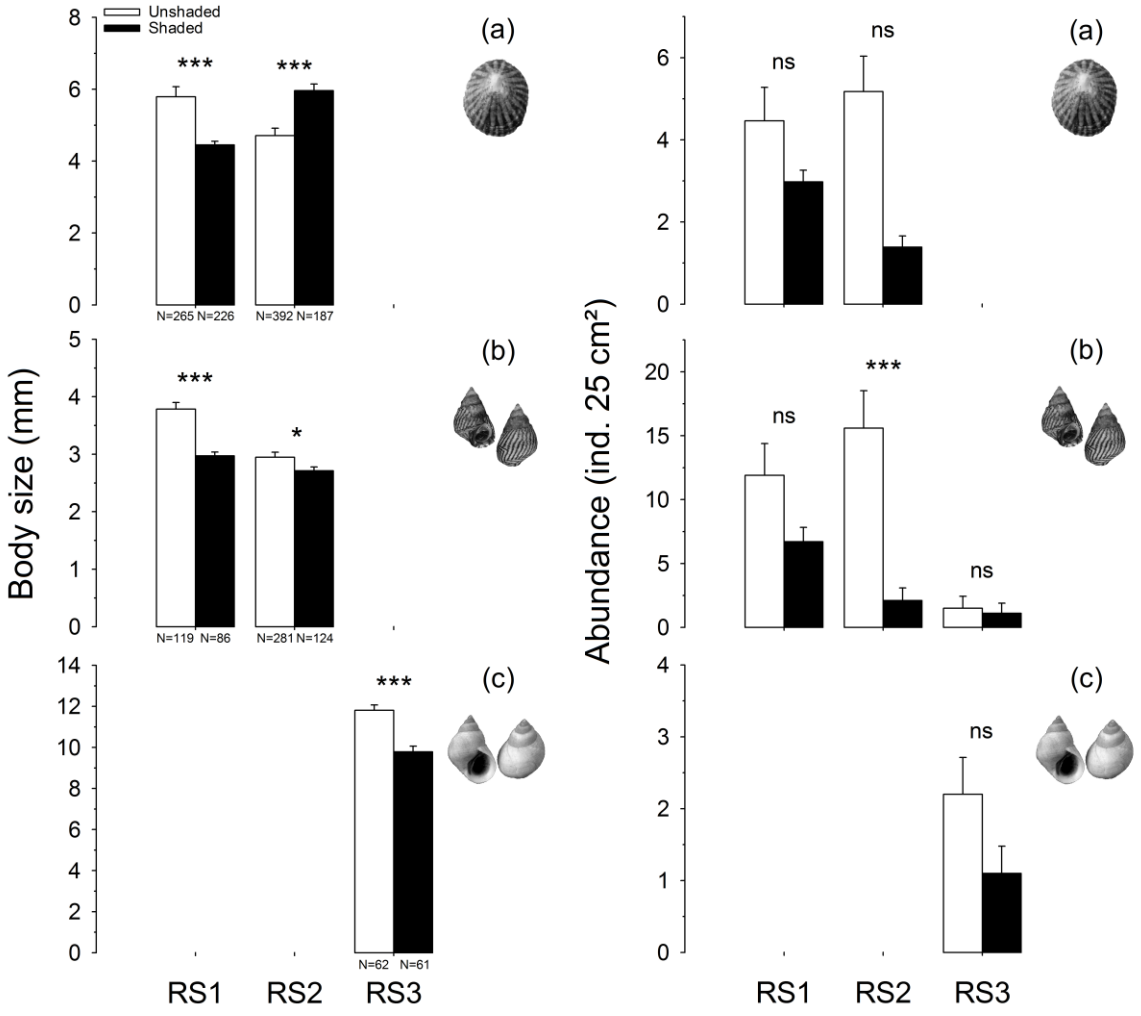


Figure 2

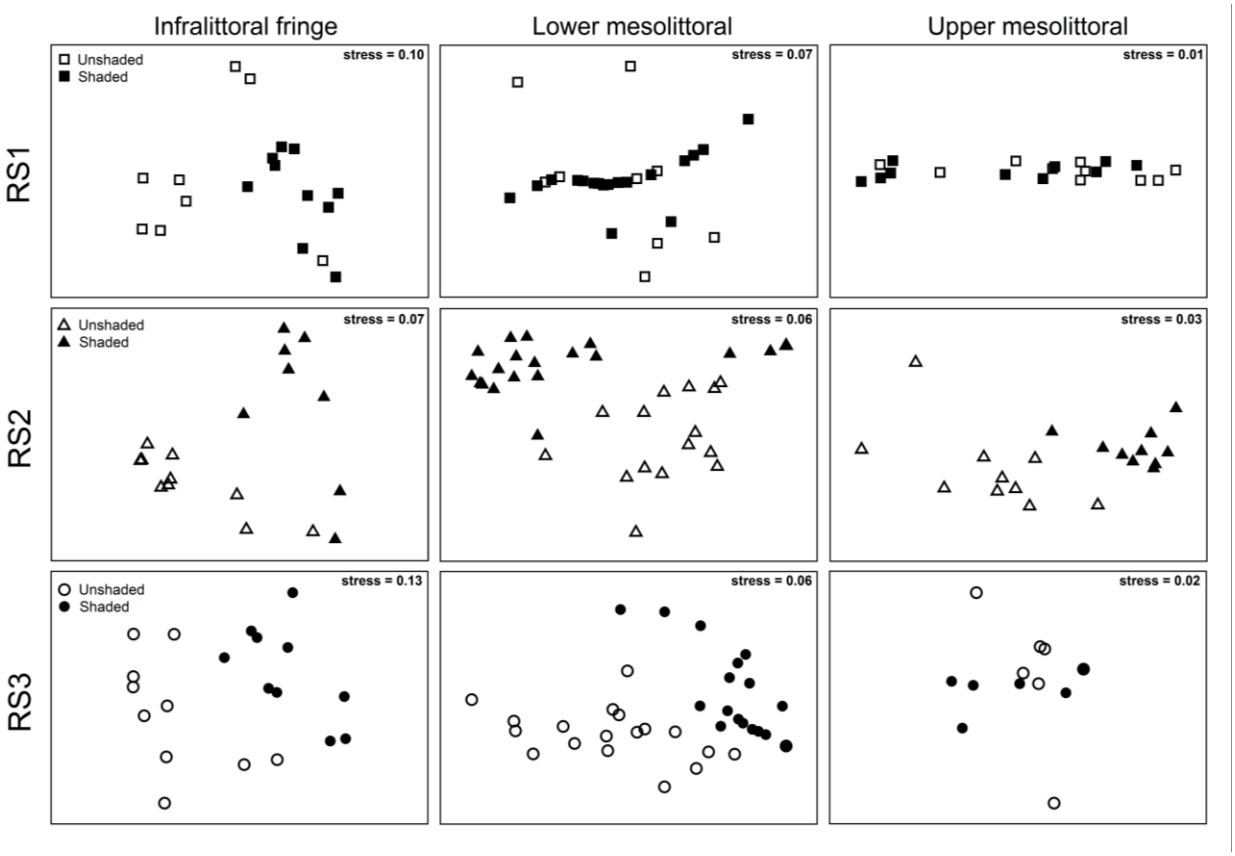

Infralittoral fringe
Lower mesolittoral
Upper mesolittoral
RS1
RS2
RS3
Unshaded
Shaded
stress = 0.10
stress = 0.07
stress = 0.01
stress = 0.07
stress = 0.06
stress = 0.03
stress = 0.13
stress = 0.06
stress = 0.02

Figure 3

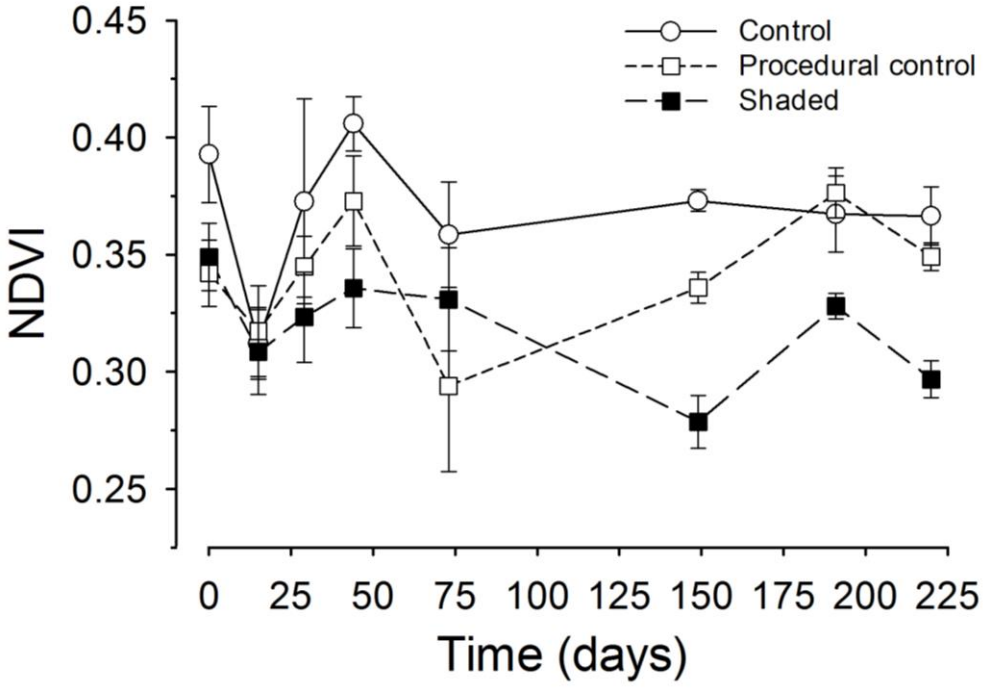

0.45
0.40
0.35
0.30
0.25
NDVI
Control
Procedural control
Shaded
0
25
50
75
100
125
150
175
200
225
Time (days)

Figure 4

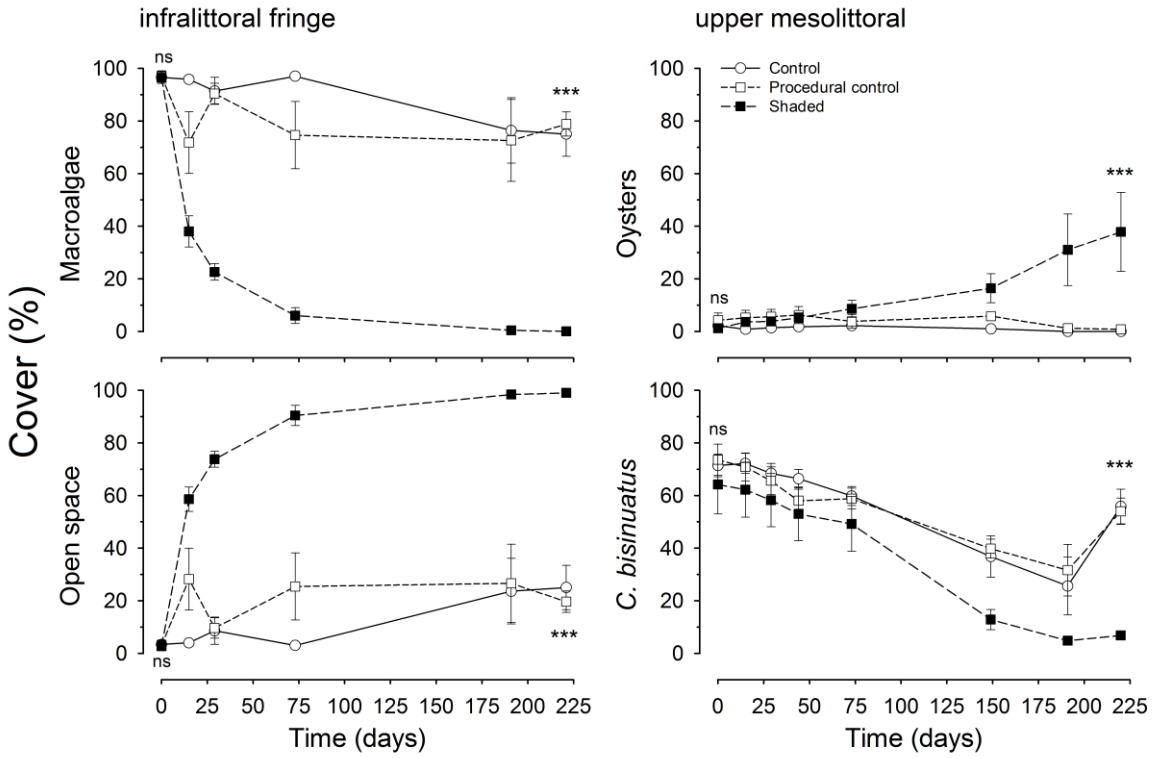
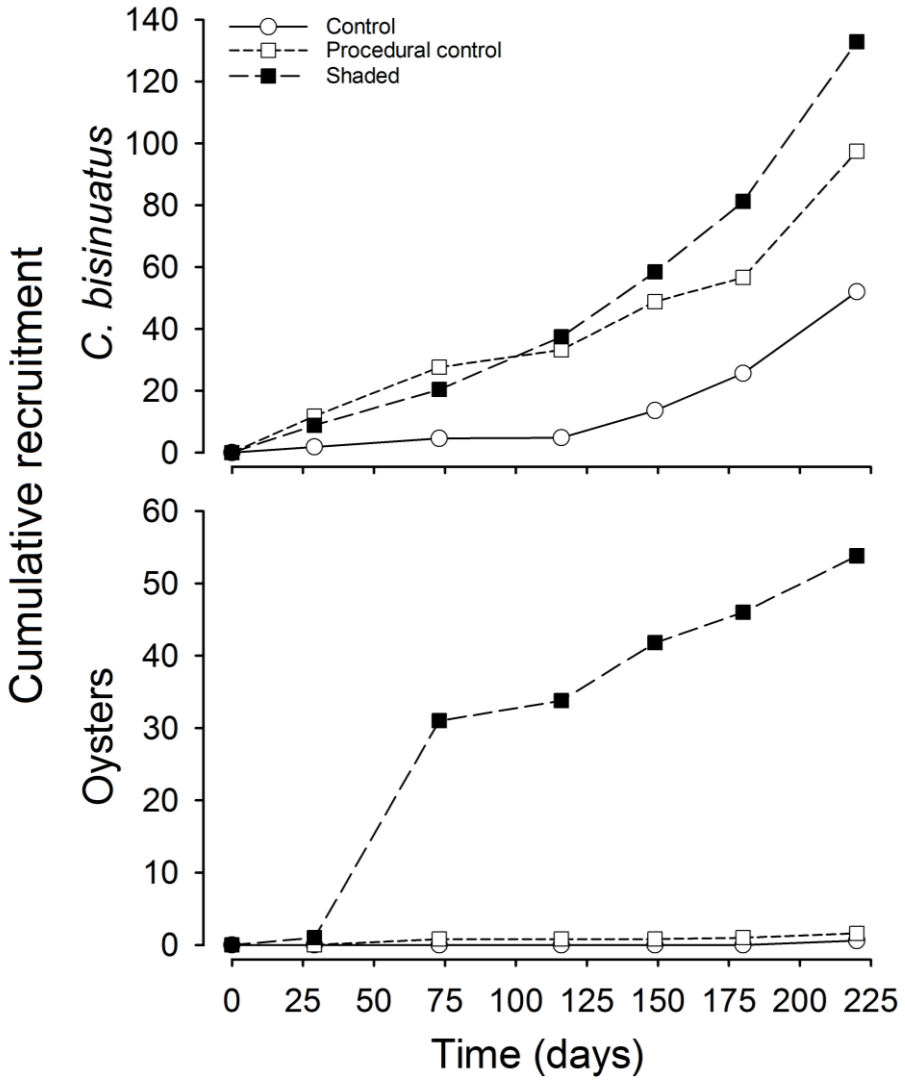

infralittoral fringe
upper mesolittoral
Cover (%)
Macroalgae
Open space
Oysters
C. bisinuatus
Control
Procedural control
Shaded
ns
***
Time (days)
0
25
50
75
100
125
150
175
200
225
0
20
40
60
80
100

Figure 5


Cumulative recruitment
C. bisinuatus
Oysters
Control
Procedural control
Shaded
140
120
100
80
60
40
20
0
60
50
40
30
20
10
0
0
25
50
75
100
125
150
175
200
225
Time (days)